Reference: *Biol. Bull.*, **145**: 200–209. (August, 1973)

CAUSES OF DAILY RHYTHMS IN PHOTOSYNTHETIC RATES OF PHYTOPLANKTON

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Rhythmic rates are characteristic of several processes in the phytoplankton. Daily oscillations are known for rates of photosynthesis (Doty and Oguri, 1957; Verduin, 1957), of chlorophyll synthesis (Yentsch and Ryther, 1957; Shimada, 1958), and rates of nutrient uptake (Goering, Dugdale and Menzel, 1964). Since the initial discovery, a number of generalizations have encouraged belief that most phytoplankton communities are rhythmic. The daily maximum in photosynthetic rate is recorded for early morning in the ocean near the equator (Doty and Oguri, 1957), for later in the day in lakes (Lorenzen, 1963), and in inshore marine environments (Newhouse, Doty and Tsuda, 1967). There is also considerable evidence that the amplitude of the daily oscillations decreases with increase in latitude (Doty, 1959).

Two categories of explanations for photosynthetic rhythms are extant in the literature, neither resolved. The first, which may be called the phasing hypothesis, is based on an intrinsic characteristic of algae, namely the ability to have cell processes entrained with a light-dark cycle. The alternative or "forcing" hypothesis is that some time dependent deficiency (nutrients) or destructive action (*e.g.*, photo-destruction) causes the oscillation.

A most cogent argument for the forcing hypothesis is based on the daily oscillation in concentrations of critical nutrients. This argument proposes that the rate of nutrient uptake is directly a function of external concentration of a rate limiting nutrient as described by Michaelis-Menten kinetics (Dugdale, 1967). Rates of uptake and growth in chemostats are offered in support (Caperon, 1967; Eppley and Coatsworth, 1968; Eppley and Thomas, 1969). Under such conditions the growth response at any concentration of nutrient would be invariant with time. Daily oscillations in photosynthesis could result, for example, from daily oscillations in nitrate and ammonium ions (Goering, Dugdale and Menzel, 1964).

The same kinetics popularized by Dugdale (1967) may be used to construct models of daily rhythms in photosynthetic potential (U_{max}). In one model the rhythm is phased to the daily rhythm of environment. In the other it is forced (Fig. 1). In the model of phased oscillation, the kinetic constants of the hyperbola oscillate (Fig. 1A). In the model of a forced oscillation, only the external concentration of a limiting nutrient oscillates (Fig. 1B).

Further analysis is possible with the models. If the phytoplankton is nutrient limited and the concentration of nutrient(s) is constant or oscillatory but with a maximum in the morning, as is characteristic, one could expect the largest response to added nutrient at some phase of the daily cycle. The timing of the maximum response to enrichment may also be expected to differ in the case of the alternative

models. The largest response to added nutrient ought to occur at the time of the daily maximum in U_{max} if U_{max} oscillates. Conversely, the largest response should be at the time of the daily minimum if the daily rhythm is caused only by an oscillation in external nutrient. Two reference points are provided in each experimental verification. One is the so-called photosynthetic capacity which is the rate of photosynthesis at light saturation or P_{max}. The second is the photosynthetic potential which is the rate at both light and nutrient saturation or U_{max}.

The first model (Fig. 1A) describes an intrinsic oscillation in the potential for photosynthesis U_{max} as shown for two time points in the daily cycle. To resolve U_{max} additional nutrient, a, is added to the existing or native (n) concentration which is constant in the model. Actual photosynthetic capacity, U, is shown as

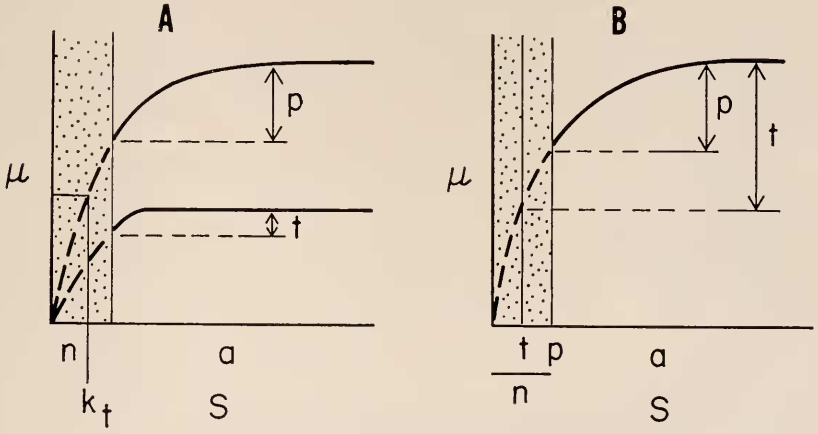

FIGURE 1. Alternative conditions permitting a diurnal oscillation in rates of phytoplankton photosynthesis. In both conditions the rate of carbon assimilation (photosynthesis) U is proportional to the external concentration of the rate limiting nutrient, S. The first condition postulates an intrinsic oscillation in U_{max} while the native (n) concentration of nutrient remains constant. The second condition postulates a constant U_{max} while the concentration of limiting nutrient forces photosynthetic rate to oscillate. See text for explantion.

two horizontal, dashed lines. At one time U is increased by "p" amount and at another by "t" amount. Note that the daily amplitude of U_{max} is greater than for U. The half-saturation constant, K_t, was held constant although it too may oscillate thereby changing the value of "p" or "t." Clearly, the intrinsic oscillation is in potential. The daily oscillation in photosynthetic capacity may be some combination of intrinsic and forced.

The second model (Fig. 1B) describes a forced oscillation in photosynthetic capacity, forced solely by an oscillation in external nutrient. The potential for photosynthesis, U_{max}, remains constant. Two points on the daily oscillation of capacity are shown by the dashed horizontal lines, the result of native nutrient, n, being at concentrations "t" and "p," respectively. Note that the addition of nutrient to resolve the hyperbola results in an increase in U by "t" and "p" amounts, respectively, and the amount of stimulation is greater at time "t" (trough) than

at time "p" (peak) or the reverse of that seen in the intrinsic oscillation. In other words two techniques are suggested for distinguishing intrinsic from forced daily rhythms in photosynthetic rates. One criterion is the behavior of U_{max} and the second is the time of day in which response to enrichment is maximum.

Methods

Rates of photosynthesis (U) were measured as rates of carbon assimilation in a standard 3-hour incubation with ^{14}C labeled bicarbonate technique (Steemann-Nielsen, 1952). Rates, corrected for excretory loss, were measured in unenriched samples and in samples to which six concentrations of sodium (primary) phosphate ranging from 0.25 to 4.0 micromoles P/liter had been added. Each experiment was

Table I

Nutrients employed to enrich water from Lake George in the second experiment

	Milligrams/liter
$NH_4 NO_3$	2.0
$Mg SO_4$	5.0
$Ca Cl_2 \cdot 2H_2O$	3.68
KCl	0.95
Fe (as $Fe Cl_3$)	0.20
$Na_2 SiO_3 \cdot 9H_2O$	1.25
Trace Elements (B, Co, Cu, Mn, Mo, Zn)	*
Vitamins	
B_1	0.0025
B_{12}	0.0001
Biotin	0.00005

* Trace elements in nanomoles/liter are H_3BO_4, 14.7, $CoNO_3 \cdot 6H_2O$, 0.7; $CuSO_4 \cdot 5H_2O$, 0.1; $McCl_2 \cdot 4H_2O$, 1.6; $H_2MO\ O_4\ H_2O$ (85%) 0.04; and $Zn\ SO_4 \cdot 7H_2O$, 0.3 nanomoles/liter.

repeated at seven different times within a 24 or 28-hour interval. One set of measurements was carried out beginning August 6 and a second on October 16, 1970.

Water for the experiments was collected from Lake George, New York (IBP-Station 1; 2 meters depth), filtered through a #25 mesh net (aperture = 64 microns), and stored in glass carboys at the lake surface but shielded from direct sunlight. The samples were incubated on a revolving drum under fluorescent light (cool white) at a saturating intensity (1500 ft-c) and at the temperature of the epilimnion (24.0° C in August and 16.0° C in October). In the second experiment replication was increased from two to three and a "complete" set of nutrients (Table I) was included as an extra treatment.

Kinetic coefficients (U_{max} and k_t) as described by the Michaelis-Menten equation were employed to characterize the growth responses, since uptake rates in both single species cultures (Eppley and Thomas, 1969) and phytoplankton assemblages (MacIsaac and Dugdale, 1968) have been shown to respond hyperbolically to the concentrations of a limiting nutrient. The linear transformation $U = U_{max} - k_t (U/S)$ was used to calculate U_{max} and k_t as recommended by Dowd and Riggs (1965) for unweighted data. Confidence limits (95 per cent) were calculated for

k_t (slope) and U_{max} (intercept). Standard errors were calculated for photosynthetic capacity which was measured in duplicate (experiment 1) or triplicate (experiment 2). The native concentration of phosphate, normally at the lower limit of detection in Lake George, was not measured. It was assumed to be 10 per cent of total phosphorus in suspension which, in August, was approximately 5.0 up P/liter (Clesceri, personal communication). The 10 per cent estimate is consistent with the estimated fraction of reactive phosphorus for many lakes (Hutchinson, 1957).

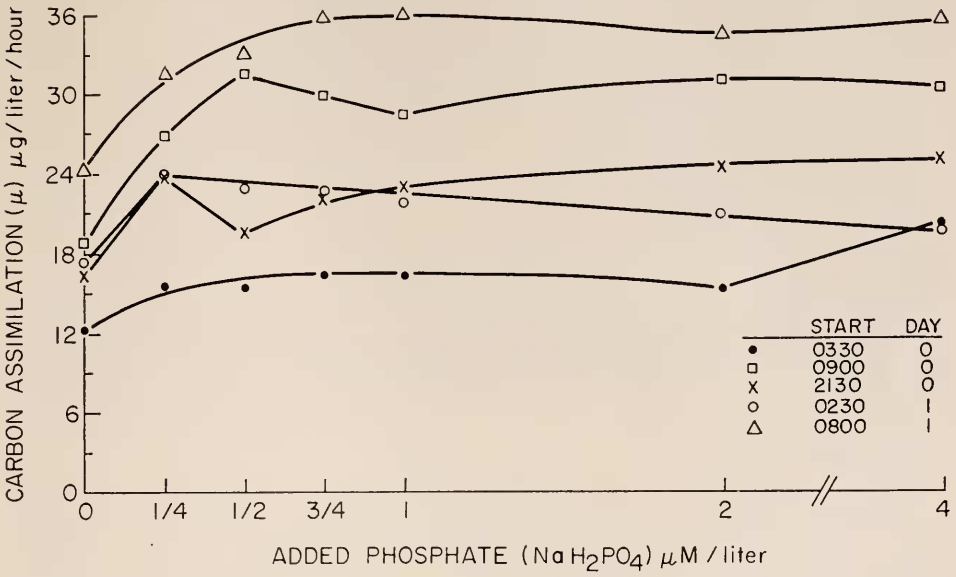

FIGURE 2. Rates of carbon assimilation in response to the addition of sodium phosphate to water samples from Lake George, New York. Shown are the results of five of seven sets of samples measured during one 30-hour interval in October 1970. Incubation was at lake temperature (16°) and at 1500 ft-c.

RESULTS

The addition of phosphate to samples of water from Lake George often but not always resulted in stimulation of carbon assimilation. In one experiment rates of carbon assimilation in five of seven sets of enrichments are shown in Figure 2. Although only a part of the total pattern can be observed, that which is the result of added phosphate is strongly suggestive of an hyperbola. Despite the general conformation, intermediate concentrations of enrichment sometimes produced slight but significant depressions in expected pattern. These so-called stalls were evident in at least two of the seven sets that comprised each experiment. While not confounding, they remind the investigator that the response of many distinct species populations is measured together.

The photosynthetic capacity, *i.e.*, P_{max} (photosynthetic rate at light saturation), of the phytoplankton in Lake George undergoes a characteristic daily oscillation.

In the first experiment (August 6) rates of carbon uptake in the unenriched samples ranged from 13.9 μg C/liter/hr at 0900 EST to 6.6 μg C/liter/hr at 2000 (Fig. 3A). Clearly the phytoplankton was most responsive to enrichment at 0900, the time of the morning maximum and least responsive at the time of the evening minimum in photosynthetic capacity. The rates were increased by 29 and 18 per cent, respectively.

Phosphate depletion in the stored sample could account for the pattern on the second morning of confinement. The oscillation in photosynthetic capacity failed to return to the same rate measured on the morning preceding (Fig. 3A). The potential or U_{max} for photosynthesis was essentially the same as the morning preceding, however, indicating that nutrients and not photosynthesizers were lacking. The rate was increased by 54 per cent on the second morning.

Photosynthetic capacities and photosynthetic potentials again oscillated in experiment 2 (October). The response was similar in essence to the first experiment although it differed in detail (Fig. 3B). Photosynthetic capacity showed a net gain of 37 per cent over a 24-hour interval. At the same time the rates of photosynthesis were much more stimulated by the addition of phosphate. The degree of stimulation was again largest at the time of the morning maximum. Photosynthesis was increased by 62.0 per cent at the morning maximum and by 27.0 per cent at the afternoon minimum. The oscillations appeared to be more irregular and photosynthetic potential showed a secondary peak in the early night. Both experiments reported here yielded the same result which in effect was that phosphate was stimulatory at all times during the experiment and thereby judged to be deficient.

Half-saturation constants

Absolute values for the half-saturation constants are unnecessary to support the model since the growth maximum is essentially independent of it. It is instructive to examine the half-saturation constants (k_t) which have been approximated with the assumption that 10 per cent of total phosphorus in Lake George water is as inorganic phosphate. Estimates of k_t in the first experiment ranged from 0.02 to 0.23 μg P/liter and in the second experiment from 0.12 to 0.30 μg P/liter. They were roughly in the range of saturation constants found for environments of inorganic nitrogen compounds in the infertile areas of the oceans (MacIsaac and Dugdale, 1968); doubling the amount of inorganic phosphate available would only double the estimates of k_t. Within each experiment the estimated constants were different. In most instances the calculated values are below the limit of resolution for phosphate in natural waters and kinetic bioassay such as proposed for glucose (Hobbie and Wright, 1965) may be appropriate.

Limiting nutrient

To reduce the possibility that the addition of phosphate was eliciting a nonnutritive response, a complete set of nutrients (Table I) was included as an additional treatment in the second experiment. The treatment was divided into two parts, one receiving all nutrients except phosphate, the second all nutrients. The experimental result was negative since at none of the seven intervals tested was the growth stimulation in response to all nutrients greater than that to phosphate only.

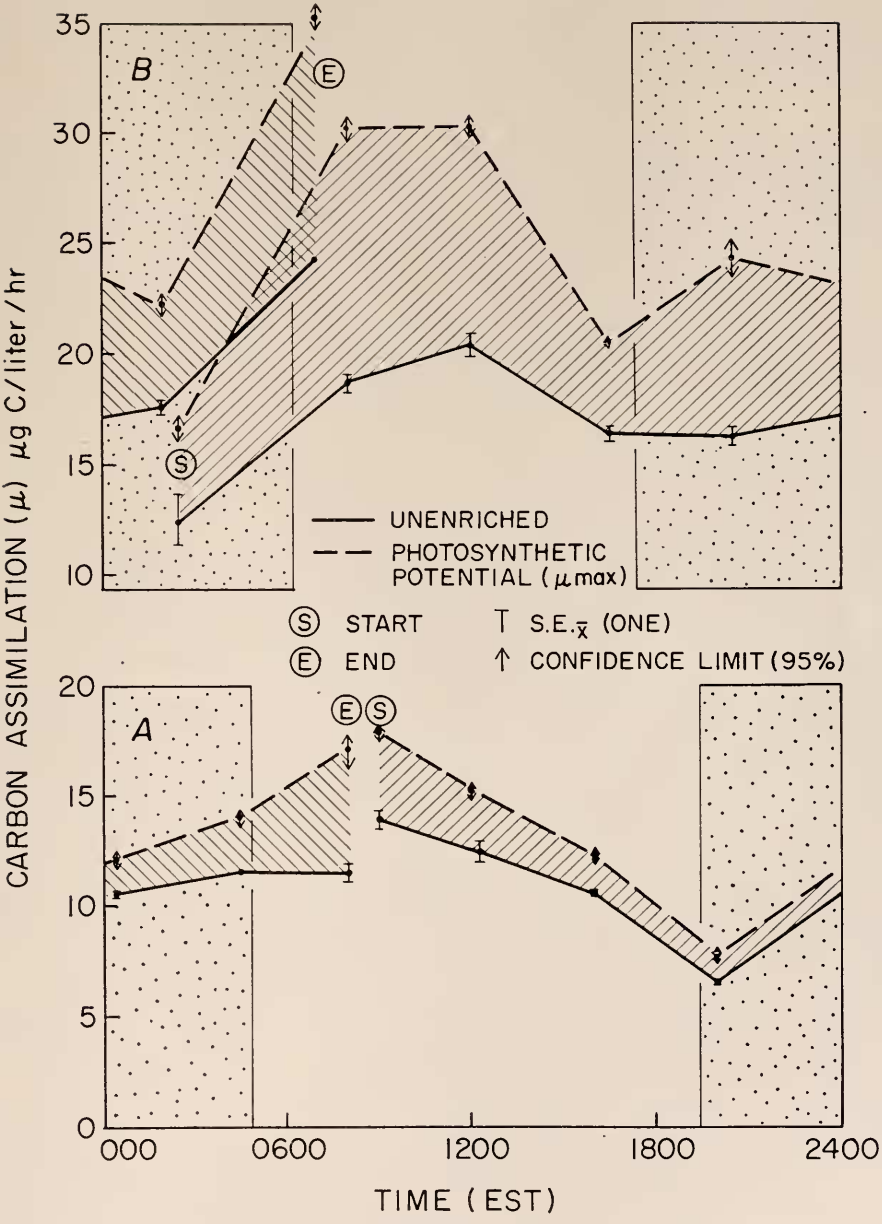

FIGURE 3. Daily rhythms in degree of stimulation achieved by the addition of phosphate to an assemblage of planktonic algae. Boundaries of the polygons were formed by rates of carbon assimilation without addition of phosphate (lower line) and a maximum rate of assimilation or U_{max} (upper boundary). Experiments performed on the phytoplankton of Lake George, New York in August (A) and October (B) 1970.

There was some stimulation in the complete minus phosphate treatment. The level of stimulation was always intermediate to that achieved with phosphate only and could indicate phosphate contamination in the other reagents.

Discussion

Photosynthetic rates of phytoplankton may oscillate each day as a result of a changing photosynthetic potential (U_{max}), or as seemed to be the case in Lake George, the rhythm may be the result of some combination of an intrinsic oscillation in potential and an oscillation in external nutrient concentration. Although the latter was unmeasured in Lake George, much evidence for a daily oscillation exists in the literature. An intrinsic basis is clearly indicated in the data, although the model itself cannot discriminate between an intrinsic rhythmicity in photosynthetic rate and the presence of a second non-nutrient forcing oscillation in the environment. The former may be the more plausible explanation. At least one dominant population, if entrained to the daily cycle, could account for a phased oscillation in photosynthetic potential. Oscillating photosynthetic capacities are characteristic of synchronous cultures (Senger, 1970) as well as cultures of algae entrained but not necessarily all dividing during the permissive or gate phase of each 24-hour cycle, *i.e.*, rhythmic (Sweeney and Hastings, 1958; Bruce, 1970). The mechanism of enrichment although light dependent is not entirely intensity dependent (Senger and Bishop, 1969). The blue-green wavelengths are the most effective at entraining cell cycles, and they are likely to be the most penetrating in clear lakes such as the lake (Lake George) on which the experiments were carried out.

Ample direct evidence for entrained cell cycles of algae in nature exists. Direct observation of dividing cells (Staley, 1971) and the oscillation in density of algal cells in the downstream drift (Müller-Haeckel, 1970) show entrained cell division cycles. An increase in the density of algal cells in suspension results apparently from loss of attachment at the time of cell division as occurs with bacteria in the field (Bott and Brock, 1970) and in culture (Helmstetter and Cummings, 1964). Cell cycles of planktonic species are also known to be entrained in nature (Eppley, Holm-Hansen and Stickland, 1968) although much of the recent evidence is less direct and in the form of activities other than cell division, *e.g.*, enzyme activity (Eppley, Packard and MacIsaac, 1970; Eppley, Rogers, McCarthy and Sournia, 1971).

There is evidence that individual rhythms of cellular activity retain a strict phase relationship (McMurry and Hastings, 1972) such that the phase of one reflects the phase of another. The potential significance of entrained cell cycles in the development of resource acquisition strategies awaits an appropriate "process" model. Eppley (1971) has already indicated the need to know the endogenous oscillation in growth (and nutrient uptake) constants (*e.g.*, U_{max} and k_t) and in the environmental oscillation in concentration of the limiting nutrient. Treatment of an entire assemblage is likely to be complicated by temporally stratified populations (phase separated rhythms of uptake) and a varying degree of coupling between carbon assimilation and nutrient uptake.

One objective of such a model may be to predict the latitudinal variation in phase and amplitude of the diurnal photosynthetic rhythm observed in the phytoplankton (Doty, 1959). In tropical waters the morning maximum was reported to be six

or more times larger than the evening minimum, whereas at high latitude it was less than two. Conceivably a model would be based on both intrinsically mediated rhythms and on forced or environmentally dictated rhythms. The consequences of shifting the phase relationship of oscillators internal and external to the alga cell are immediately obvious. If for example the uptake of a limiting nutrient and photosynthetic fixation of carbon are oscillatory with the former driving the latter, phase of the two would determine the amplitude of the daily rhythm in photosynthetic capacity. The amplitude would be progressively damped if the photosynthetic maximum was shifted to later in the day while the nutrient uptake maximum remained in the early morning.

Conceivably, the latitudinal pattern, *i.e.*, the loss of amplitude and apparent shift of the maximum in photosynthetic capacity to later in the day, is due in part to such a mechanism. Doty and Oguri (1957) discovered the maximum to be at dawn in tropical areas. Lorenzen (1963) and Newhouse *et al.* (1967) found late morning to midday maxima at temperate latitudes. Phytoplankton in temperate latitudes may be most responsive to nutrient addition (this paper) and to thermal stimulation (Morgan and Stross, 1969) at midmorning or midday. However, we found arctic phytoplankton to be most responsive to thermal pulsing in late afternoon and evening (unpublished). If indeed the phasing of endogenous rhythms within the cells of algal populations can account for amplitude and phase changes with latitude, there is reason to expect other insights from a model.

In the simple analysis above the assemblage is viewed as a single species when an assemblage of many species exists reach conceivably with a unique rhythm. Coexistence of potential competitors gives statistical evidence that competition is avoided (Hutchinson, 1961). Unique phase and amplitude characteristics of growth (Hastings and Sweeney, 1964) and uptake kinetics of co-dominant species have been suggested as one mechanism for avoiding or minimizing competition in an environment where nutrient resource inputs are continuous (Williams, 1971; Eppley *et al.* 1971). Conceivably temporal uniqueness in nutrient uptake is a feature of the co-dominant populations in a phytoplankton assemblage. A model containing sufficient detail of the endogenous characteristics of co-dominant populations, if viewed over a wide range in photoperiods (or latitude), may well provide insight into the significance of endogenous rhythms. For the moment at least it is sufficient to suspect that field rhythms are a compromise between a forcing oscillation in the environment and an inherent rhythmicity in potential of the organisms (Enright, 1970).

Field experiments conducted at the lakeside laboratory of Freshwater Institute of Rensselaer Polytechnic Institute. Work supported in part by USIBP EDFB with funds from NSF through AEC: AG-199, 40–193–69.

Summary

The cause for the daily rhythm in the photosynthetic capacity of phytoplankton has been examined. Alternative hypotheses have been modeled with the Michaelis-Menten equation. In one model rates of photosynthesis oscillate in response to a forcing from the external concentration of limiting nutrient while photosynthetic

potential (U_{max}) of the assemblage remains constant. In the alternative model photosynthetic potential oscillates in response to intrinsic organization of the cell. The alternatives may be deduced from the photosynthetic response to added nutrient.

The photosynthetic response to added phosphate was tested with water from Lake George, New York. Rates of carbon assimilation in the unenriched controls described a daily oscillation with an amplitude of approximately two and a phase maximum in midmorning. The degree of stimulation to added phosphate was also rhythmic. The maximum and minimum corresponded with the daily maximum and minimum, respectively, in unenriched controls. The oscillating intensity of response was interpreted as a changing potential in the intrinsic capacity of the algal assemblage.

The display of intrinsic rhythms by at least one dominant component in the algal assemblage infers the entrainment of activity cycles to the daily cycle. Additional evidence to support the inference is described. Although the algae may be entrained, there is also evidence from the literature that nutrient concentrations undergo daily oscillations. Photosynthetic rhythms could result from both an intrinsic and a nutrient (forcing) oscillation. A changing phase relationship between the two could explain the decline in amplitude of the photosynthetic rhythm with increase in latitude.

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